

# Mechanistic drivers of cyanobacterial dominance and eukaryotic algal decline in estuarine ecosystems: integrating nutrient stoichiometry and thermal stratification

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## Abstract

Cyanobacteria in estuarine ecosystems outcompete eukaryotic algae through the synergistic interaction of nutrient flexibility, buoyancy control, and thermal stratification. Although these changes in the ratio of nitrogen to phosphorus (N: P) are usually detrimental to eukaryotic taxa, specific cyanobacteria either fix atmospheric nitrogen (N<sub>2</sub>) or can store phosphorus, and are able to grow during nutrient-limited phases. This review identifies critical low N: P thresholds and temperature ranges that trigger a shift from diatom-rich to cyanobacteria-dominated states. Rising global temperatures and stratification of water columns aid the utilization of gas vesicles and help cyanobacteria to reach the surface, where they absorb sunlight and effectively suppress competing organisms. Their high tolerance to warmer water and formation of toxins protect them against grazing pressures that normally regulate the algal populations. The resulting feedback loop involves thick cyanobacterial mats which increase surface temperatures and cause hypoxia through decomposition, which in turn leads to loss of biodiversity and collapse of existing algal-based food web. These findings provide a mechanistic predictive framework for estuarine management, emphasizing that climate-induced warming necessitates more stringent, dual-nutrient (N and P) reduction targets to prevent the onset of toxic monocultures.

**Key words:** CyanoHAB, dead zones, estuaries, food web disruption



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## Introduction

The study investigates the causes and outcomes of cyanobacterial dominance and algal decline in estuarine ecosystems (Balaji Prasath et al. 2014; Sukenik and Kaplan 2021). Combining the evidence regarding nutrient dynamics, physiological adjustments and environmental feedback this study gives us a holistic perspective of the processes involved and the solutions that can be adopted in regulating the ecosystem. The literature review was conducted based on its relevance to the three core mechanisms, namely, nutrient stoichiometry (N: P ratios), thermal stratification, and allelopathic interactions. Primary producers,

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which are predominantly eukaryotic algae and cyanobacteria, are essential for aquatic ecosystems in sustaining the higher trophic levels of the food web (Saleem et al. 2025). Eukaryotic algae include the highly complex organisms such as diatoms and chlorophytes that contain organelles that are bound by membranes and specialized chloroplasts. They serve as the preferred feed for zooplankton and fish; thus, they function as the primary energy sources as they effectively transform solar energy and dissolved nutrients into high-quality biomass (Weinstock et al. 2022). Cyanobacteria on the other hand are early-evolved prokaryotes, which do not have a nucleus, but possess diverse evolutionary adaptations. Although they share the same photosynthetic niche as the eukaryotic algae, their cell structure is simpler, compensated by, and augmented by specialized adaptations, such as gas vesicles that enable vertical movement and heterocysts to fix nitrogen (Mehdizadeh Allaf and Peerhossaini 2022). These prokaryotic competitors are the first to respond to environmental fluctuations and proliferate into dominant bloom-forming species. The replacement of eukaryotic algae-dominated ecosystem by cyanobacteria is an indicator of significant deterioration of the health of estuaries (Zhang et al. 2022). Anthropogenic nutrient release and global warming raise the temperature of the water column, provide a competitive edge for the robust growth of cyanobacteria. This regime shift is not merely a change in species composition, it represents a transition to an ecosystem that is less diverse, potentially toxic, and prone to the hypoxic dead zones. Although the literature has recorded the stressors that affect an individual organisms, there is no combined study of the interaction between thermal stability and nutrient stoichiometry. This compounding effect, in which thermal stratification magnifies the benefits of nutrients, is the focus of this review to discuss the mechanisms underlying the limitations of current management. This review focuses on estuarine case studies that report both physical stratification data and chemical nutrient ratios. The aim is to get beyond species-specific accounts of competition and identify universal mechanistic. Patterns of competitive displacement. In order to study this transformation in a systematic manner, the review is organized in three core mechanism, namely, nutrient stoichiometry, physical stratification and allelopathic inhibition.

### Nutrient shifts and buoyancy: rise of cyanobacteria over algae

This shift is examined through the factors enabling cyanobacteria to dominate in estuarine habitats. The increase in cyanobacteria is driven by the changes in the nutrient stoichiometry, especially the nitrogen to phosphorus (N: P) ratio. For instance, a study in 2012 on *M. aeruginosa* bloom in Muttukkadu Backwater (Tamil Nadu, India), recorded high phosphate (15.57  $\mu\text{mol/L}$ ) and ammonia (54.97  $\mu\text{mol/L}$ ) under stagnant conditions (salinity 0 ppt), which resulted in densities of  $6 \times 10^8$  cells/L, outcompeting algae via N-fixation. Due to excessive phosphorus loading in most estuaries, nitrogen acts as a limiting role for eukaryotic algae (Balaji Prasath et al. 2021). Cyanobacteria overcome nitrogen limitation through heterocysts that enable them to fix atmospheric nitrogen ( $\text{N}_2$ ) into a usable form. This provides a competitive advantage by enabling sustained biomass production during periods of nutritional limitation and rising water temperatures. Cyanobacteria possess gas vesicles that support active buoyancy regulation, unlike eukaryotic algae, which rely on the turbulence of

the water to remain in the photic zone (Wu et al. 2023). Cyanobacteria move to the surface, in the stratified, stagnant waters of a degraded estuary, resulting in dense scums. This provides a competitive advantage by allowing them to obstruct light availability shading out the eukaryotic algae underneath, effectively displacing them for the fundamental resource in the aquatic habitat: light. The intensification of chemical and physical stresses is also a threatening factor for the community structure (Vione and Rosario-Ortiz 2021). Cyanobacterial blooms may cause the water to become extremely alkaline (typically above 9.0 with a rapid depletion of  $\text{CO}_2$ ) stressful conditions for many eukaryotic algae. In addition, the synthesis of secondary metabolites (cyanotoxins) leads to allelopathic inhibition, directly suppressing the growth of other phytoplankton. The combination of these toxins and the unpalatable colonial form of cyanobacteria results in a grazing resistance in which the zooplankton preferentially feed on beneficial algae thus further impacting the decline of the original community. Ultimately, these environmental pressures form a positive feedback mechanism that solidifies the domination of cyanobacteria. This increases the competitive challenge for the eukaryotic algae as the water grows warmer and more stagnant and resulting in the loss of the productive season and the deterioration of estuarine health (Paerl 2014). The resulting monoculture is highly unstable; when such large blooms finally die, they decompose in the water column expending all the dissolved oxygen. This results in critical hypoxia which inhibits the restoration of the algal community while also causing mass mortality of species in higher trophic levels, such as fish and benthic invertebrates (Fig. 1).

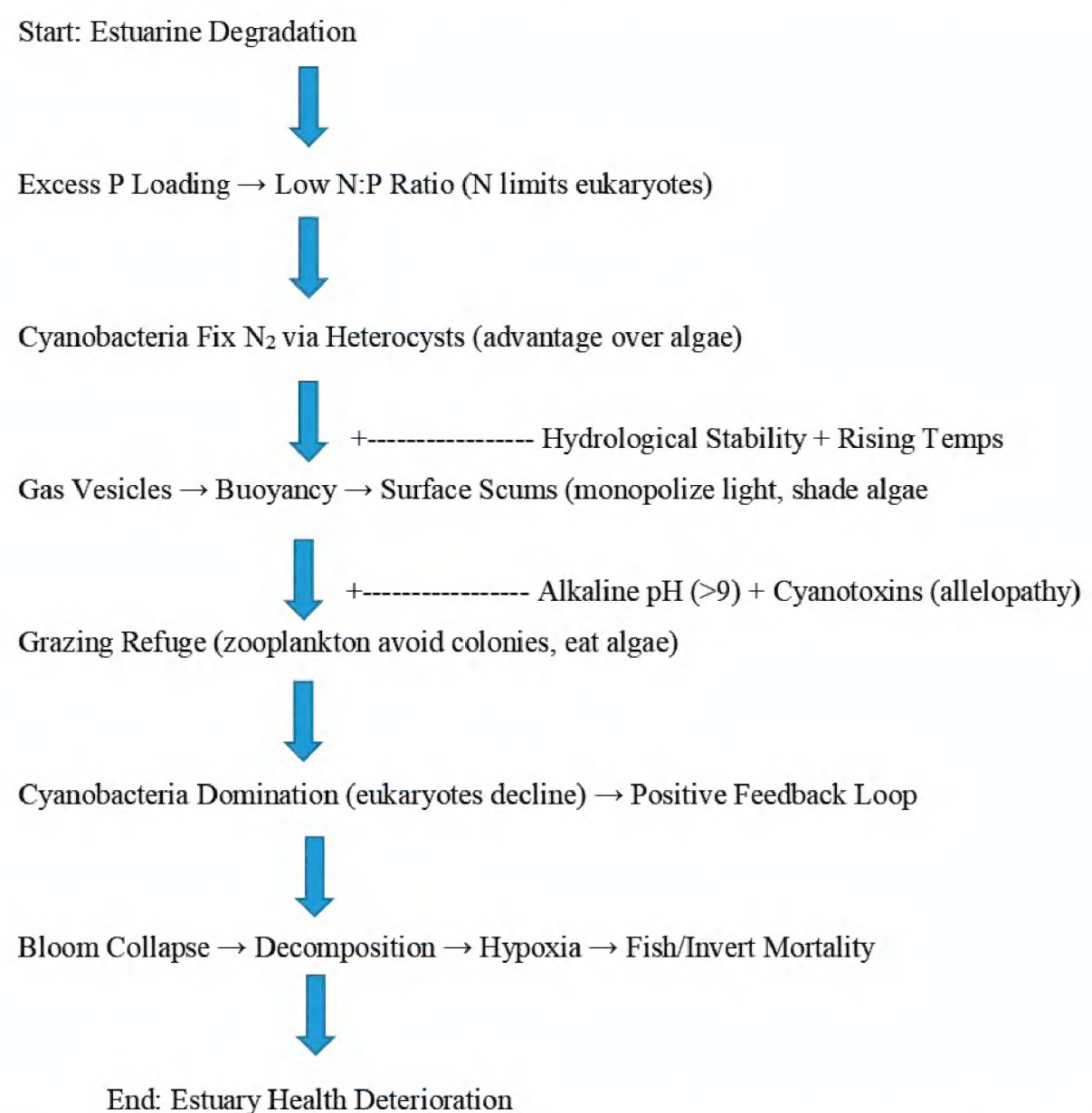


**Figure 1.** Conceptual flowchart illustrating the transition from estuarine degradation to cyanobacterial dominance, driven by P-loading and low N:P stoichiometry Mechanisms behind Algal Decline

A synergistic ecological mechanism combining resource acquisition and allelopathic inhibition renders eukaryotic algae vulnerable to cyanobacterial dominance. The core of this change lies in fundamental shifts in the dynamics of nutrients and light. Cyanobacteria can photosynthesize even in the turbid and muddy waters of an estuary due to the wider range of light-harvesting pigments (including phycobiliproteins) (Hemlata and Fatma 2009). They form a physical canopy of gas vesicles floating on the surface and effectively shade out the eukaryotic algae a few meters beneath it by obstructing incoming solar radiation. Furthermore, cyanobacteria fix nitrogen ( $N_2$ ) and thrive under nitrogen- and phosphorus limited conditions ( $N:P < 16:1$ ), outcompeting algae despite imbalanced stoichiometry (Barathan et al. 2023). Several dominant species, including *Microcystis* sp. and *Anabaena* sp. release secondary metabolites and certain cyanotoxins (e.g. microcystins) into the surrounding waters. These biochemicals not only harm fish; they function as allelochemicals that inhibit the physiological processes of competing microalgae. These allelochemicals have been shown to affect the photosynthetic electron transport chain, damage cell membranes and inhibit enzyme activity in eukaryotic algae, resulting in slower growth or complete collapse of algal populations (Śliwińska-Wilczewska et al. 2019). Such chemical inhibition tends to suppress recovery even when nutrients are available existing algal populations remain physiologically impaired. The most significant component of this competitive advantage is the feedback loops that the specific metabolism of the cyanobacteria has developed. Due to their prolific photosynthesis, they significantly elevate the pH of the water greatly and dissolved inorganic carbon is depleted, making the water alkaline and inhospitable to the majority of eukaryotic life (Singh et al. 2016). Also, their toxin-containing colonies are not palatable, reducing zooplankton from grazing. This creates a top-down pressure, as grazers selectively consume the rest of the competitive algae, in effect reorganizing the ecosystem to make the cyanobacteria dominant. The result is an estuarine habitat in which the eukaryotic communities are shaded out at the surface, are excluded from the photic zone, and chemically suppressed physiologically (Fig. 2).

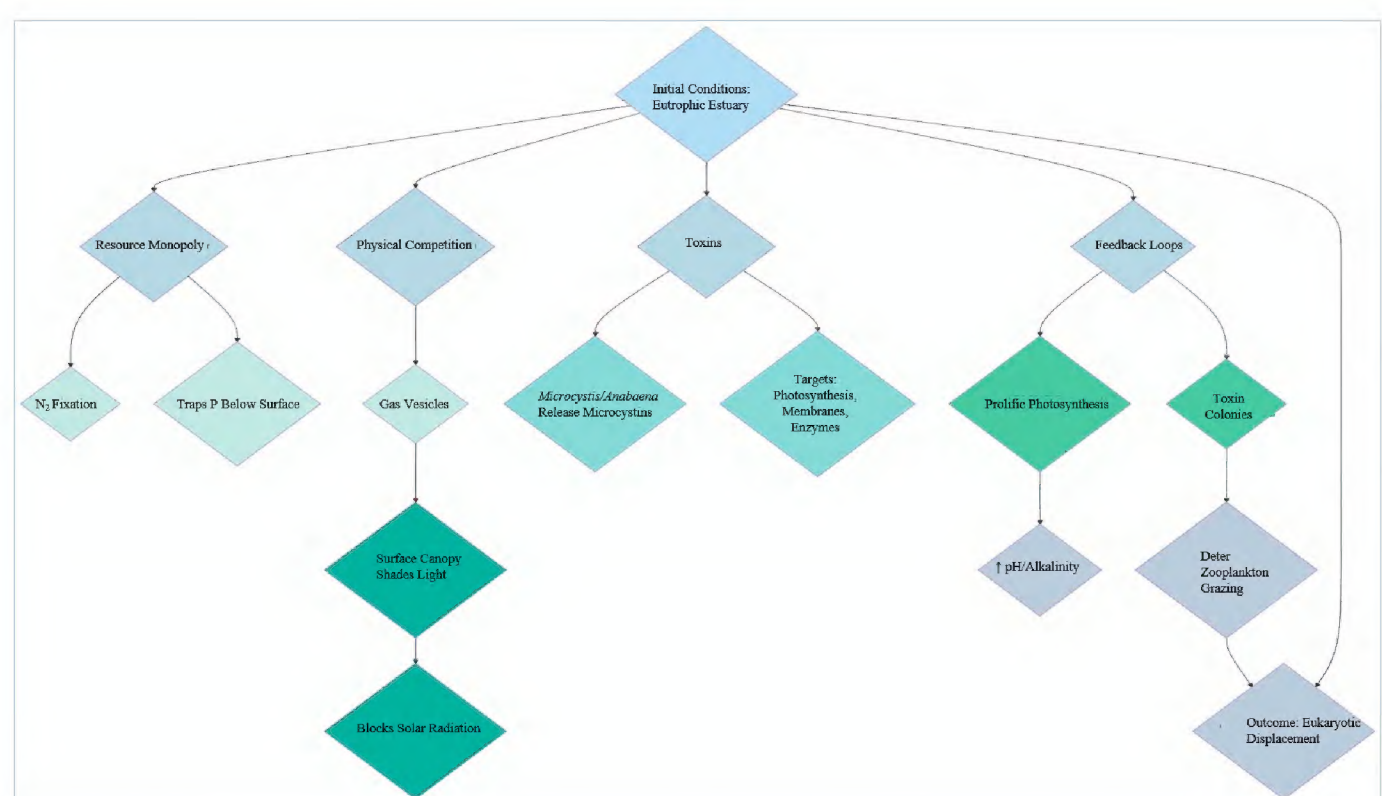


**Figure 2.** Integrated pathways of eukaryotic displacement, highlighting the synergy between physical competition (shading) and biochemical inhibition (allelopathy).

## Ecosystem collapse and management strategies

Cyanobacterial succession is linked to a disastrous collapse in estuarine food webs and water quality. The poor nutritional quality, and toxicity of cyanobacteria, whose presence interferes with the growth and reproduction of zooplankton, the link between primary producers and the higher trophic levels. This trophic bottleneck results in starvation that causes the juvenile fish mortality and shellfish declines and the bioaccumulation of the cyanotoxin, hepatotoxins and neurotoxins that directly threaten the life of the aquatic organisms and people consuming the fish and shellfish. Moreover, the ultimate death and decay of these extensive blooms result in extreme hypoxia/anoxia which creates so-called dead zones, where dissolved oxygen levels drop dramatically causing the mass mortality of benthic organisms and fish. This bloom caused massive fish kills due to microcystin hepatotoxins and oxygen depletion post-decay, mirroring estuarine dead zones and underscoring pollution from effluents as a bloom trigger. To effectively control such blooms, there is a need to move beyond reactive measures based on chemical treatment and adopt proactive watershed-wide management that addresses the underlying causes of nitrogen (N) and phosphorus (P) enrichment (Nwankwegu et al. 2019). The traditional P-only reduction techniques are not effective in the estuaries that have nitrogen-fixing cyanobacteria that need more integrated dual-nutrient reduction techniques to re-establish the N: P ratio at a more optimal state to encourage favorable algae growth. In addition to nutrient control, physical manipulations such as artificial circulation, periodical release of freshwater to promote flushing and recovery of natural hydrological flows are more important to disrupting the vertical stratification that favors buoyant cyanobacteria species. (Stroom and Kardinaal 2016). The interaction between warming and nutrients loading is synergistic rather than merely additive. For example, higher temperatures increase the metabolic demand for phosphorus in eukaryotic algae, increasing their sensitivity to the low N: P ratios that cyanobacteria exploit through N-fixation. Consequently, as global temperatures rise, estuarine nutrient thresholds must be lowered to prevent the formation of cyanobacteria scums. Dual-nutrient (N and P) reduction and physical actions such as artificial circulation should be prioritized. Further, future management should aim to limit the thermal niche, which provides them a competitive advantage. The interaction between eutrophication and climate change is highly complex and leads to increased deterioration of estuarine health. Rising global temperatures and increased incidences of extreme weather conditions such as excessive rainfall and prolonged periods of dry seasons will tend to expand the bloom period and intensify the cyanobacterial outbreaks (Zepernick et al. 2021). To make the ecosystem resilient in the long run, future management should incorporate early-warning systems and predictive modeling that considers the shifting climatic variables. Scientific perspectives in the future need not be confined to mitigation of the bloom, but should be coupled with the ecological health of the estuaries to enable them to support the ecological diversity of algal communities supporting healthy and productive coastal ecosystems.

## Conclusion

The dominance of cyanobacteria in estuarine ecosystems has resulted from a complex process of competitive displacement, driven by anthropogenic perturbations. The most interesting finding is that these prokaryotes have physiological capacity to regulate their buoyancy by using gas vesicles, fixation of nitrogen and in the production of allelopathic metabolites to specifically inhibit eukaryotic algae. With a self-reinforcing feedback as a result of monopolizing the surface light and surviving in low N: P conditions, cyanobacteria degrade water quality, leading to hypoxia and disruption of energy transfer through the food web. Such a change in the heterogeneous algal community towards the toxic monoculture is an indicator of a lack of ecological stability, and nutrient over-enrichment and the rise in temperature around the world are working synergistically. Despite this, the literature still shows major gaps on the long-term consequences of salinity rise on the toxicity of some cyanobacterial strains and the survival of eukaryotic algae during non-growing periods of blooms. Future research should focus on creating high-resolution, multi-stressor models, which will be able to indicate how alterations in precipitation patterns and the rising in sea levels will affect the estuarine flushing and nutrient stoichiometry. The second course of action is to develop novel bio-restoration methods, including the deployment of specialized clay flocculants or the reintroduction of native filter-feeders, to actively prevent blooms while simultaneously, implementing watershed-scale nutrient reductions. It is imperative that these gaps be addressed in order to shift from reactive management of crises to the proactive recovery of the estuarine biodiversity. The primary takeaway for stakeholders is that the shift to toxic monocultures implies loss of ecological resilience. Proactive recovery requires a transition from reactive chemical treatments to watershed-scale nutrient stoichiometry management that specifically targets the disruption of the cyanobacterial surface-canopy advantage.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

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No ethical statement was reported.

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## Author contributions

R. Nanda Kumar: Writing-original draft, Methodology, Collection, Formal analysis, Resources, Validation, Data curation. M. Jayaprakashvel: Writing- review & editing, Investigation, Supervision, and B. Balaji Prasath: Conceptualization, Writing- review and editing, Supervision, Validation, Visualization.

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## Data availability

All of the data that support the findings of this study are available in the main text.

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